

NEOTROPICAL BUTTERFLIES OF THE GENUS *ANARTIA*:
SYSTEMATICS, LIFE HISTORIES AND GENERAL
BIOLOGY (LEPIDOPTERA: NYMPHALIDAE)

BY ROBERT E. SILBERGLIED¹

ANNETTE AIELLO¹

AND

GERARDO LAMAS²

INTRODUCTION

Butterflies of the genus *Anartia* Hübner are among the most common and conspicuous diurnal Lepidoptera encountered in the New World tropics. While their abundance and ease of capture have made them popular subjects for research in various aspects of lepidopteran biology, the genus has never been thoroughly reviewed or revised. Two of the authors, (R.E.S. and A.A.) have been conducting genetic, behavioral and ecological experiments on members of this genus for four years, and we feel it is both an opportunity and a necessity to condense the scattered published information with some of our own observations and results. Our experimental findings will be published separately.

As treated here, *Anartia* consists of five species (Figure 1) in three well-defined groups (Godman and Salvin, 1882).

SYSTEMATICS

Genus *Anartia* Hübner

Anartia Hübner, [1819]: 33.

Type species, *Papilio jatrophae* Linnaeus (Scudder, 1875: 111).

Celaena Doubleday, [1849]: 214.

Type species, *Papilio fatima* Fabricius (Hemming, 1941: 425). Invalid and unavailable; published in synonymy (ICZN, Art. 11d).

Celoena Boisduval, 1870: 38.

Type species, *Papilio fatima* Godart (mon.). Junior subjective synonym.

Anartia subgenus *Anartiella* Fruhstorfer, 1907: 112.

Type species, *Vanessa lytrea* Godart (mon.). Junior subjective synonym.

¹Smithsonian Tropical Research Institute, Box 2072, Balboa, Republica de Panamá.
Present address: Museum of Comparative Zoology, Harvard University, Cambridge,
Mass. 02138

²Museo de Historia Natural "Javier Prado," Universidad Nacional Mayor de San
Marcos, Av. Arenales 1256, Aptdo. 1109, Lima, Perú.

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Medium-sized, lightly built butterflies. *Head* small; *eyes* hemispherical, prominent; *labial palpi* elongate, curved upwards and densely scaled, with first and third segments about 1/4 to 1/3 the length of the second (Reuter, 1896, fully describes the palpi); *antennae* slender, slightly shorter than the body in length, with slightly flattened, pointed, nine-segmented club; *thorax* strong, thinly scaled; *forewing* slightly angled apically, anterior margin curved at base, apex slightly truncate, outer margin sinuate, inner margin straight, Sc-R system variable among the species (Figure 2; Doubleday, 1849; Schatz, [1887]; Godman and Salvin, 1882), costal cell open; *hindwing* somewhat quadrate, longer than wide, produced distally into a slight tail at vein M3, veins Rs, M1 and M2 diverging nearly from the same point, costal cell open; *prothoracic legs of male* thin, tibia longer than the femur, a single tarsomere half the length of the tibia, clothed in fine white setae; *prothoracic legs of female* thicker than those of the male, tibia shorter than the femur, five tarsomeres, together nearly equalling the tibia in length, each tarsomere bearing stout spines, especially the apical one; *meso- and metathoracic legs* long, femora shorter than tibiae, tibiae and four basal tarsomeres spiny, claws moderately curved; *abdomen* equal in length to head and thorax combined; *male genitalia* (Figure 3) with a bifid, curved uncus and simple valves. *Chromosome number*, $n=31$ (*A. amathea*, *A. fatima* and *A. jatrophae*; Maeki and Remington, 1961; Wesley and Emmel, 1975).

Scudder (1893) suggests that the generic name is derived from the Greek for "incongruous; in allusion to its great difference in marking from its fellows." Glaser (1887) states that *Anartia* is a "prince of the caste of the children of the sun" (Indian mythology). The only common name used for the genus as a whole is "the American Peacocks" (Brown and Heineman, 1972).

Anartia amathea and *A. fatima*

Anartia amathea (Linnaeus)

amathea (Linnaeus), 1758: 478 (*Papilio*).

Type locality: ["Indiis."]

[*amalthaea* (Clerck), 1764: pl. 40, fig. 3. Emendation; see below.]

amalthaea (Cramer), 1780: 29, 173, pl. 209, fig. A, B.

Unjustified emendation; see below.

roeselia (Eschscholtz), 1821: 207, pl. 5, fig. 9 (*Cynthia*).

Type locality: "Brasil."

silvae Burmeister, 1861: 168.

New synonymy.

Type locality: Argentina, Tucumán, Manantial de Marlopa.

amathea subspecies *sticheli* Fruhstorfer, 1907: 101.

Type locality: Bolivia, "5 days north of Cochabamba."

amathea subspecies *thyamis* Fruhstorfer, 1907: 102.

Type locality: Brasil, São Paulo; Santa Catarina; Rio Grande [do Sul]; "Paraguay."

[*amathea* subspecies *roeselia* aberration "conjuncta" Zikan, 1937: 387.

Type locality: Brasil, Minas Gerais, Passa Quatro, 900 m.]

Linnaeus may have committed a 'lapsus calami,' or mistransliterated *amathea* from Greek to Latin. The etymologically correct spelling is *amalthea*, for the goat that nursed Jupiter. (The reddish, innermost satellite of the planet Jupiter is also named Amalthea.) Clerck's emendation was followed by Cramer, and used by many others since then, but *A. amathea* must stand as the *nomenclaturally* correct name, since there is no "clear evidence of an inadvertent error" by Linnaeus (ICZN, 32 (a) (ii)), and no "demonstrably intentional change in the original spelling" by Clerck (ICZN, 33 (a)). Clerck's names have no standing in nomenclature, as he did not use the binomial system. The etymology of *amathea* is discussed in greater detail by Fruhstorfer (1907).

Anartia fatima (Godart)

fatima (Godart), [1824]: 375 (*Nymphalis*).

Type locality: "des Indes." Suggested replacement for *fatima* Fabricius. See below.

fatima Fabricius, 1793: 81 (*Papilio*).

Type locality: "Indiis." Junior homonym of *Papilio fatima* Cramer, 1780.

Application for suppression of this name has been forwarded to the ICZN.

See below.

fatima subspecies *venusta* Fruhstorfer, 1907: 111.

Type locality: "México," "Guatemala."

moreno Kruck, 1931: 234, fig. 1.

Type locality: México, Oaxaca. Aberration.

fatima form *albifasciata* Hoffman, 1940: 281.

Type locality: "México".

[*fatima* aberration "albifusa" Hoffmann, 1940: 281, fig. 6, 7.

Type locality: México, Veracruz, Tierra Blanca.]

[*fatima* subspecies *venusta* form "colimensis" Hoffmann, 1940: 283, fig. 5b.

Type locality: México, Colima; [Michoacán], Río Balsas.]

[*fatima* aberration "oscurata" [sic] Maža, 1976: 103, fig. 1.

Type locality: México, Veracruz, Cerro El Vigía.]

[*fatima mirus* Martin, 1923: 54.

Type locality: Paraguay. Nomen nudum.]

If we were to follow strictly the rules of zoological nomenclature, *A. fatima* (Fabricius), as a junior primary homonym of the riodinid *Emesis fatima* (Cramer), would be invalid, since they were both described in the genus *Papilio*. However, considering the large amount of biological information published on this species, it would be in the best interest of a stable nomenclature if the specific epithet could be conserved. Accordingly, we have applied to the International

Commission on Zoological Nomenclature, for conservation of the name *fatima*, by recommending that the use of the name *fatima* Fabricius be suppressed until 1824, when Godart transferred the species to the genus *Nymphalis*. This would not affect the nomenclature of the rioidinid, and would have the advantage of keeping the name *fatima* in use for what is certainly the most familiar Central American butterfly. The synonymy presented here reflects this recommendation.

The name *fatima* was first used in *Anartia* in 1837, by Geyer, in Hübner [1824-]1825[-1837] (see Hemming, 1937, p. 479).

Anartia amathea and *A. fatima* (Figure 1) are a pair of very closely-related species, restricted to the tropical and subtropical mainland of Latin America, including Trinidad and offshore islets. The ranges of these species abut in eastern Panamá (Darién); hybrids between them have been collected in the field at the juncture of their distributions on several occasions (e.g., Brown, 1975). Intensive study of the mortality and development of F1 hybrids (Figure 4) and their offspring reveals strong hybrid breakdown, and behavioral research on courtship and mating preferences reveals a complex picture of assortative mating. These results and their evolutionary consequences will be reported elsewhere; we here want to emphasize that we interpret *amathea* and *fatima* as biologically separate species.

The wing venation, male genitalia and larvae of *amathea* and *fatima* are, so far as we have been able to tell, identical. The wing venation (Figure 2) differs from that of other members of the genus by the two small veins that leave the Sc-R complex and branch towards the costa in the forewings. The valvae of the male genitalia (Figure 3) lack the basal swellings and sharp ventro-medial spines characteristic of *chrysopelea* and *lytrea*, and are similar to, but more lanceolate than, those of *jatrophae*.

A. amathea is easily distinguished from all other members of the genus by the extent of its vivid red coloration. On the dorsal surface, the red coloration extends into two spaces between the four postbasal/submedian lines of the anterior forewing, fills the median area of the posterior forewing, the submedian and median area of the hindwing (except for a dark line running through it from anterior to posterior), and the hind submarginal area of the hindwing. There are usually three to four subapical, five postmedial and four submarginal white spots on the forewing, and from one to four small submarginal white spots on the hindwing. The basal and postbasal regions of the wings are brown; all other markings are dark brown to black.

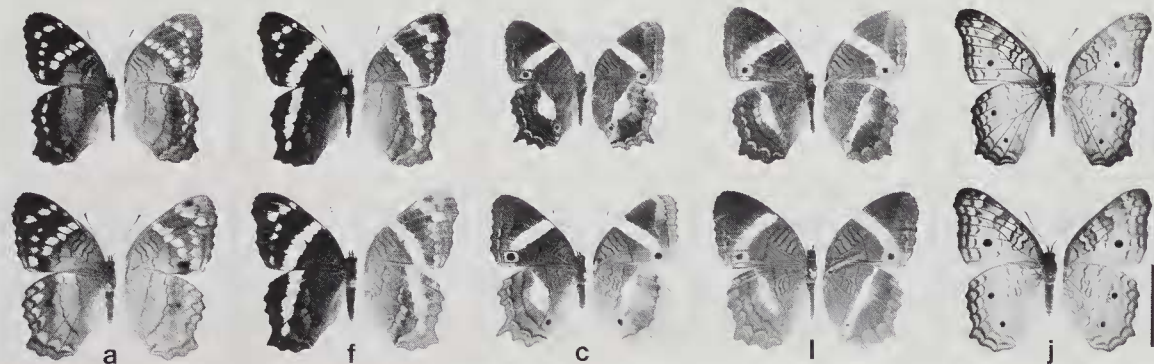


Figure 1. Adult butterflies of the genus *Anartia* (male above, female below). a = *A. amathea* [male: stock from Panamá, Darién Prov., Río Sambú, ex ovum, lot no. 107, ind. no. A-436, 1976, reared on *Blechnum brownei*, R. E. S. & A. A.; female: same as male, except lot. no. 99, ind. no. A-434]; f = *A. fatima* [male: Panamá, Zona del Canal, Barro Colorado Is., ex ovum, ind. no. 78-52-14, 1978, reared on *Blechnum brownei*, A. A. & R. E. S.; female: same as male, except ind. no. 78-52-17]; c = *A. chrysopelea* [male: Cuba, Sierra Maestra, 1,000 ft., 23 Nov 1929, O. Querci; female: same as male, except 21 Sep 1930]; l = *A. lytrea* [male: Hispaniola, Haiti, coll. F. E. Church [AMNH]; female: Hispaniola, Rep. Dom., Santo Domingo, ex coll. J. Doll, Ac. no. 24352 [AMNH]]; j = *A. jatrophae* [male: Panamá, Zona del Canal, Barro Colorado Is., ex ovum, ind. no. 79-133-H, 1979, reared on *Lindernia diffusa*, A. A. & R. E. S.; female: same as male except ind. no. 79-133-E]. Scale = 2 cm.

The pattern is similar but much paler on the ventral surface. Most of the markings that are black dorsally are brown ventrally. There are, in addition, two dark postmedian spots, an elongate one in forewing cell Cu2 and a small, round one in hindwing cell M1. The saturation of the red color, and the overall contrast of the pattern, is more pronounced among males than among females, especially on the dorsal wing surfaces. The red color is noticeably faded on older individuals and on old museum specimens.

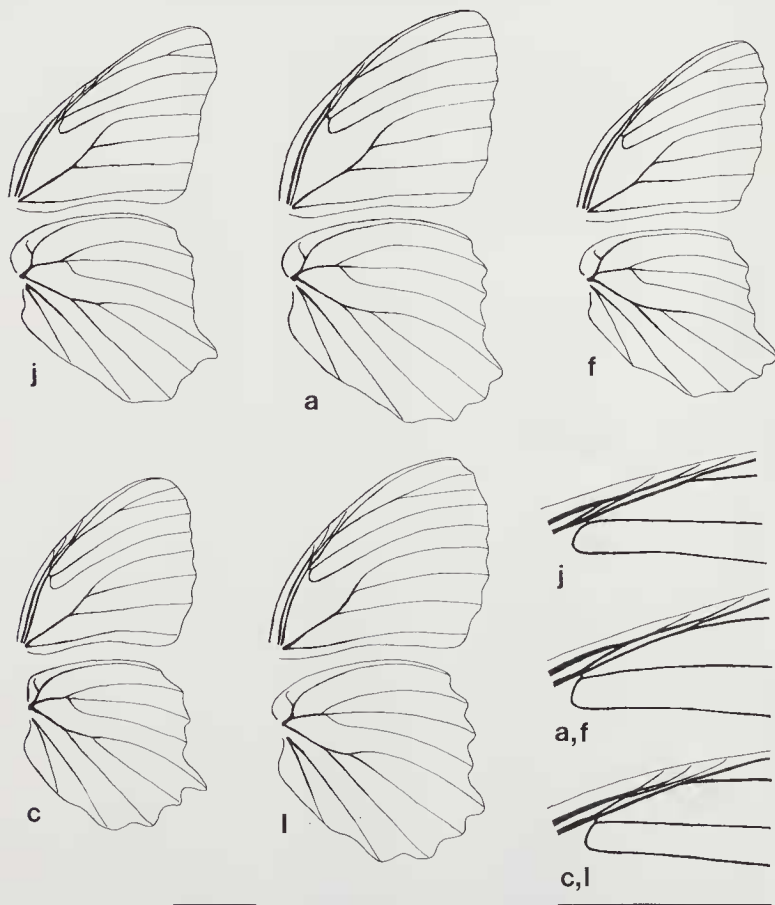


Figure 2. Wing venation of the five species of *Anartia*. a = *A. amathea*, f = *A. fatima*, c = *A. chrysopelea*, l = *A. lytrea*, j = *A. jatrophae*. Scales = 1 cm. See text.

Specimens of *A. amathea* from the southeastern part of its range are characterized by fusion of the five postmedian forewing spots into a broad, white band. Examination of large numbers of specimens reveals that this spot fusion exhibits much variation both within and between populations, and forms a cline running from northwest to southeast (Figure 5). Accordingly, we recognize Eschscholz' "roeselia" simply as that end of the cline showing the most distinctive forewing banding, not as a subspecies. Burmeister's "silvae," and Fruhstorfer's "thyamis" and "sticheli," are poorly-characterized variants that fall well within the ordinary range of variation.

Several common names have been coined for *amathea*, including the "Coolie" (Barcant, 1971), the "Tomato" (Kaye, 1921), and the "Red *Anartia*" (Riley, 1975).

The wing pattern of *A. fatima* is built around elements similar to those of *A. amathea*, but modified and colored in such a manner as to produce quite a different appearance. The wings are dominated by the distinctive bands, composed in the forewings of seven, and in the hindwings of five, enlarged postmedian spots, fused with one another. When *A. fatima* is at rest, the forewing and hindwing bands are joined in a continuous line. *A. fatima* also has three to four subapical and one to four submarginal spots on the forewing, of the same color as the band. The red coloration is restricted to a narrow median band on the hindwing (composed of four spots, distal to the position of the dark median line of *A. amathea*), and along the hind margin in some specimens. The remainder of the wings is largely dark brown to black, including the spaces between the four black postbasal/submedian lines on the anterior forewing. The ventral surface is similar in pattern to, but much lighter than, that of the dorsum; the bands are occasionally infuscated with darker scales beneath, and there is usually a well-developed, black, postmedian c-shaped mark in hindwing cell M1 just basal to the band. Males and females have similar patterns, but that of the male is generally more saturated and of higher contrast than that of the female.

The color, nature and function of the distinctive bands of *A. fatima* have been subjects of much research. In all populations, individuals can be found with yellow bands, white bands, or any shade from yellow to white. Fruhstorfer (1907) considered the white-banded form to be a distinct subspecies, *venusta*. Emmel

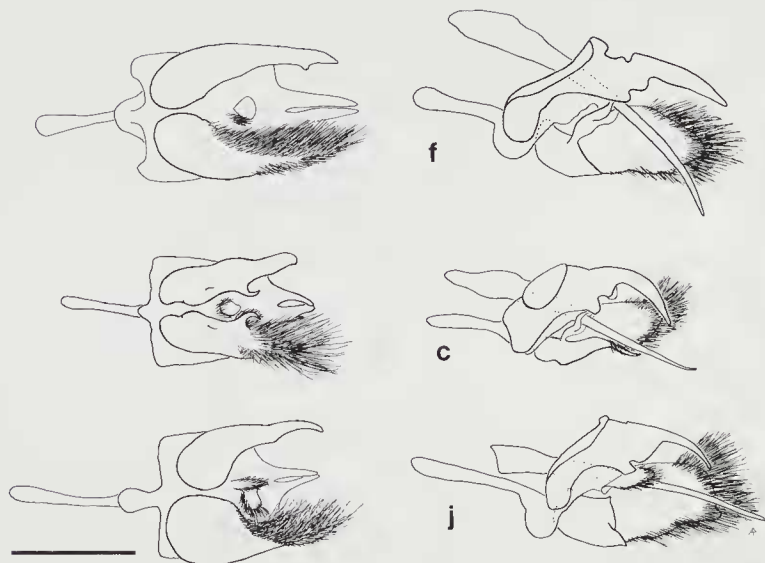


Figure 3. Male genitalia of the three species-groups of *Anartia*. Left: ventral view; Right: lateral view with left valve removed. Scale = 1 mm. [Specimen data: *A. fatima*: Panamá, Zona del Canal, Barro Colorado Island; *A. chrysopelea*: "Cuba"; *A. jatrophae*: Colombia, Cali.]

(1972, 1973), assuming that the band color differences had a genetic basis, reported "phenotype" frequencies, as well as behavioral experiments designed to learn more about the maintenance of such a polymorphism. Taylor (1973) disputed Emmel's assumptions, demonstrating that the band color was age- and sex-related, and correlated with physical and physiological measures of age. Young and Stein (1976) showed that the band colors, of marked individuals in a population, fade with time; they also reported some equivocal data on the colors of individuals at eclosion.

Our own (R.E.S. and A.A., in prep.) studies, which include rearings of over a thousand individuals, and the following of over a thousand marked individuals in a natural population, will be reported in detail elsewhere. But our clear-cut results are relevant to a consideration of the nature of Fruhstorfer's *venusta* and can be summarized as follows: Males *always* eclose with clear yellow wing-bands ($N=1119$). The color of the female wing-bands at the time of eclosion is variable, and may be anywhere in the continuum from

yellow to white; it appears to be independent of the length of the period of larval and pupal development. The bands of males, and of females that are not already white, always fade to white over a period of approximately two weeks under natural conditions. Fading appears to be related to light exposure; it can be induced in dead specimens exposed to sunlight (Taylor, 1973), but does not occur in museum specimens protected from light.

A. fatima shows marked variation in the extent of red coloration on the hindwings, with an increasing expression of red on the hind margin of the hindwing, in the northwestern part of its range. Hoffmann's "colimensis" (Figure 5) represents the extreme expression of red in *A. fatima*. There is an intriguing resemblance between this variant of *A. fatima*, and the banded "roeselia" of *A. amathea*, at the northern and southern extremes of their respective ranges.



Figure 4. F1 hybrids of *A. amathea* and *A. fatima*, male above, female below. Reared on *Blechnum brownnei* at Barro Colorado Is., Panamá. Left: *A. amathea* female x *A. fatima* male: male AF-17, 1977, female AF-160, 1976. Right: *A. fatima* female x *A. amathea* male: male FA-151, 1976, female FA-274, 1976.

Several other variants of *A. fatima* have also been reported or described, most of which are well within the normal phenotypic range. The more unusual forms include Kruck's "moreno" (a melanic lacking the characteristic band), and Hoffmann's striking "albifusa" (with the forewing band extending toward and fusing with the subapical white spots). Aiello and Silberglie (1978) reported, but did not describe taxonomically, an aberration with orange instead of red hindwing markings³, apparently due to the homozygous condition of a recessive allele at a single locus. A similar, probably homologous aberration apparently exists in *amathea* (A. Shapiro, pers. comm.).

The only common name we know for *A. fatima* is simply "Fatima" (Klots, 1951).

F1 hybrids between *amathea* and *fatima* are illustrated in Figure 4. These reared specimens closely resemble those captured by G. B. Small, K. S. Brown (1975), and ourselves at several localities in eastern Panamá where the two distributions are contiguous. The two reciprocal hybrids are intermediate between the parental species, and similar to one another, in color and pattern, and there is relatively little variation among the offspring of either cross. A paper illustrating and describing the F1, backcross and F2 generations, and discussing the interspecific genetics of pattern characters, is in preparation.

Anartia chrysopelea and *A. lytrea*

Anartia chrysopelea Hübner

chrysopelea Hübner, [1831]: 34, pl. [95], fig. 547, 548.

Type locality: Cuba, La Habana.

[*litraea*, Herrich-Schäffer, 1864: 163.

Misspelling.]

lytrea subspecies *eurytis* Fruhstorfer, 1907: 112 (*Anartia* (*Anartiella*)).

Type locality: "Haiti (?), Puerto Rico (?)."

Anartia lytrea (Godart)

lytrea (Godart), 1819: 299 (*Vanessa*).

Type locality: unknown; "de l'expédition du capitaine Baudin."

dominica Skinner, 1889: 86.

Type locality: Haiti, [Artibonite], Samana Bay.

³We have since found that the red color of normal *fatima* (and *amathea*) can be changed to orange, identical to that of this aberration, by immersing the wings in dilute hydrochloric acid.

These two species, endemic to the largest islands of the West Indies, are very similar to one another and evidently closely related. They are identical in wing venation and genitalic structure, and differ only slightly in size, wing shape and wing pattern. Seitz (1924) and Bates (1935) considered them to be subspecies ('choromorphs' of Bates). However, since there is little variation within each of these entities, since the differences between them are very consistent, and since they are well-isolated geographically, they are evidently *biologically* separate species and are so treated here.

The venational features that distinguish these species are the combination of a single vein crossing from R to Sc, and three veins



Figure 5. Above, variation among specimens of *A. amathea* in the expression of postmedial forewing banding. Specimen data, from left: Colombia, Villavicencio, Dept. Meta, 588 m, 28 Sep 1942, M. Bates; Peru, La Merced; Brasil, Rio del Janeiro, Brasil, Pelotas, C. Biezanko ["roeselia"]. Below: A western Mexican specimen of *A. fatima* illustrating extreme expression of dorsal hindwing red coloration, and ventral infuscation of the band. Specimen data: México, Colima, Jacob Doll coll. ["colimensis"].

branching from Sc toward the costa in the forewing (Figure 2). The male genitalia (Figure 3) are very distinctive, with a pronounced basal swelling and ventro-medial spine on each valve.

A. chrysopelea is the smallest member of the genus, and has the most strongly developed "tail" at hindwing vein M3. The dorsal ground color of the wings is very dark brown, the males being darker than the females. A 2-3 mm wide, white postmedian band crosses the forewing, similar to that of *A. fatima* but composed of only five fused postmedian spots, and extending only to Cu2. Each hindwing bears an oval to rhomboid median white macula. A round 'ocellus' (eye-spot), consisting of black ringed with dull orange, is located in the anal angle of both fore- and hindwing, that of the forewing being slightly larger than that of the hindwing. The fine, dark, postbasal and submedian lines are present but obscured. Both wings have a series of dull orange submarginal lunules.

The ventral ground color is lighter; the hindwing macula is infuscated and crossed basally by a narrow stripe that extends from the costal margin to, and nearly surrounding, the 'ocellus.' The ventral forewing 'ocelli' are of the same relative size as they are dorsally. Occasional specimens have a suffusion of lavender scales postmedially in the ventral hindwing.

A. lytrea is somewhat larger than *A. chrysopelea*, with lighter brown ground color and less distinct markings. Dorsally, the white bands are slightly infuscated, with less sharply defined edges. Those of the hindwings are more elongate, and not as wide in the middle. The orange ring surrounding the 'ocellus' in the anal angle of the forewing is much wider in *A. lytrea*, and the hindwing 'ocelli' are far smaller than the forewing 'ocelli.' As in *A. chrysopelea*, there is a narrow row of submarginal orange lunules, more strongly curved in *A. lytrea*. The underside pattern is modified in a way similar to that of *A. chrysopelea*, but in the hindwing the orange ring does not quite surround the 'ocellus.' The "tail" at hindwing vein M3 is not as pronounced in *A. lytrea* as in *A. chrysopelea*.

A. chrysopelea and *A. lytrea* have been called "Huebner's Anartia" and "Godart's Anartia," respectively (Riley, 1975).

Anartia jatrophae

Anartia jatrophae (Linnaeus)

jatrophae ([Linnaeus] in Johansson), 1763: 25 (*Papilio*).

Type locality: "America"; Surinam (Munroe, 1942: 2).

corona Gosse, 1880: 199, pl. 8, fig. 1.

Type locality: Paraguay, "near Asunción." Aberration.

saturata Staudinger, [1885]: pl. 39, fig. [6] [as species]; [1866]: 104 [as variety].

Type locality: Haiti, Port-au-Prince; "Puerto Rico."

jatrophae variety *jamaicensis* Möschler, 1888: 27.

Type locality: "Jamaica."

[*jatrophae* aberration "margarita" Oberthür, 1896: 30, pl. 9, fig. 18.

Type locality: Brasil, Bahia.]

jatrophae subspecies *luteipicta* Fruhstorfer, 1907: 112.

Type locality: "Honduras."

jatrophae variety *pallida* Köhler, 1923: 24, pl. 2, fig. 12.

Type locality: Argentina, Misiones.

jatrophae subspecies *luteopicta* Munroe, 1942: 2.

Type locality: Honduras. Incorrect spelling, not available.

jatrophae subspecies *guantanamo* Munroe, 1942: 2.

Type locality: Cuba, Oriente, Guantánamo, San Carlos Estate.

jatrophae subspecies *semifusca* Munroe, 1942: 3.

Type locality: Puerto Rico, San Juan.

jatrophae subspecies *intermedia* Munroe, 1942: 4.

Type locality: "St. Croix."

The name *Jatrophae* (which may be a misnomer based on Merian's [1705] erroneous larval foodplant association) has been attributed to Johansson, but we agree with Hodges (1971, p. 29-30) that authorship should properly be ascribed to Linnaeus.

A. jatrophae has the widest geographic range of any species in the genus. Morphologically, it is distinctive in the combination of two veins crossing separately from R to Sc, and three veins branching from there to the costa (Figure 2). The male genitalia (Figure 3) are most similar to those of *A. amathea* and *A. fatima*, but have blunter and slightly asymmetrical valves.

A. jatrophae has a distinctive appearance that sets it apart from the other species. The ground color of most of the wings is dirty white or light gray, with marginal and submarginal dull, rusty orange in some populations. The wings often have a pearly lustre, especially beneath. The pattern is quite complex and highly variable in the tone of pigmentation, distal ground color and expression of certain details. Besides the intricate series of dark lines, chevrons and lunules in the lighter field (better studied in the photographs then described), there are three characteristic postmedian dark spots: a large one in forewing cell Cul and others in hindwing cells M1 and Cul.

The ventral surface is much lighter in ground color, and even more variable than the dorsum. There are often red-orange submar-

ginal lunules, and edgings of the same color on the lines in the ventral hindwing. The center of the dark spot in hindwing cell M1 is often suffused with blue scales.

Geographic and seasonal pattern variation in *A. jatrophae* have been the subjects of several papers (e.g., Munroe, 1942; Gillham, 1957; see also Longstaff, 1912). Consideration of large numbers of specimens from many localities and dates reveals an unusually large amount of phenotypic plasticity in pattern detail, both geographic and seasonal. The "several recognizable but not easily defined subspecies" (Riley, 1975) were the subject of a careful quantitative investigation by Gillham (1957), who concluded that they resulted from discordant variation in several characters. Although several modern authors (Brown and Heinemann, Howe, Klots, Riley, etc.) continue to recognize subspecies in *jatrophae* (especially for the West Indian populations), we see no reason to do so. They are better referred to as "*jatrophae* from . . ." than by taxonomic epithets that substitute for knowledge of the factors underlying their variation.

Common names used for *A. jatrophae* include the "White Peacock" (e.g., Holland, 1898; Klots, 1951; Riley, 1975; Rawson, 1976) and the "Biscuit" (Barcant, 1971).

BIOLOGY

ADULT BEHAVIOR AND ECOLOGY

Habitats, seasonality and population structure

Species of *Anartia* are found wherever their larval foodplants occur. Feeding as they do on herbaceous tropical weeds (Table 1), they are restricted to well-watered, disturbed habitats. Under natural conditions, these would include flood plains, landslide areas, treefall gaps, and similar sites, to 2,000 m or more, depending on latitude.

Human activities benefit *Anartia*. Their foodplants grow well along irrigation and drainage ditches, and large populations are found along roadsides, and in agricultural situations, throughout most of Latin America (see Young and Muysshondt, 1973; Young and Stein, 1976). *Anartia* are frequently found flying in the company of *Junonia* spp., with whom they have several larval foodplants in common. *A. jatrophae* appears to succeed in drier sites, and those with lower vegetation (e.g., Leck, 1974), where foodplants not utilized by the other species grow. In seasonally dry areas, populations usually diminish in size during the months of little rainfall

Table 1. Larval foodplants reported for *Anartia* species.

FOODPLANT SPECIES	FAMILY	USED BY	LOCALITY	REFERENCE
	Acanthaceae	A	Brasil	Müller (1886)
<i>Blechnum brownei</i>	Acanthaceae	A	Colombia	A.A. & R.E.S.
<i>Blechnum brownei</i>	Acanthaceae	A, F, J	Panamá	A.A. & R.E.S.
<i>Blechnum brownei</i>	Acanthaceae	F	Costa Rica	Young & Stein (1976)
<i>Blechnum pyramidatum</i>	Acanthaceae	F	Costa Rica	Young & Muyschondt (1973)
<i>Blechnum pyramidatum</i>	Acanthaceae	F	Costa Rica	Young & Stein (1976)
<i>Blechnum costaricense</i>	Acanthaceae	A, F	Panamá	A.A. & R.E.S.
<i>Justicia candalerianae</i>	Acanthaceae	F	Costa Rica	Young (1972)
<i>Dicliptera unguiculata</i>	Acanthaceae	F	Costa Rica	Young & Stein (1976)
<i>Jacobinia magnifica</i>	Acanthaceae	A	Brasil	cited in Lima (1967-1968)
<i>Ruellia occidentalis</i>	Acanthaceae	J	?	cited in Howe (1975)
<i>Ruellia tweediana</i>	Acanthaceae	A	Brasil	cited in Lima (1967-1968)
<i>Melissa officinalis</i>	Labiatae	A	Brasil	cited in Lima (1967-1968)
<i>Melissa officinalis</i>	Labiatae	J	Brasil	cited in Lima (1967-1968)
<i>Mentha piperita</i>	Labiatae	J	Brasil	cited in Lima (1967-1968)
<i>Mentha pulegium</i>	Labiatae	J	Brasil	cited in Lima (1967-1968)
<i>Lippia citriodora</i>	Verbenaceae	J	Brasil	cited in Lima (1967-1968)
<i>Lippia</i> sp. ¹	Verbenaceae	J	Florida	Scudder (1892)
<i>Lippia</i> sp.	Verbenaceae	J	Florida	A.A. & R.E.S.
<i>Lippia</i> sp.	Verbenaceae	J	Cuba	Gundlach (1891)
<i>Lippia</i> sp.	Verbenaceae	J	Cuba	Dethier (1941)
<i>Lippia</i> sp.	Verbenaceae	C	Cuba	Dethier (1941)
<i>Bacopa monniera</i>	Scrophulariaceae	J	Florida	Rawson (1976)
<i>Bacopa monniera</i>	Scrophulariaceae	J	Puerto Rico	Wolcott (1951)
<i>Lindernia diffusa</i>	Scrophulariaceae	J	Panamá	A.A. & R.E.S.
<i>Jatropha manihot</i> ²	Eurphorbiaceae	J	Surinam	Merian, Sepp, . . .

¹ Riley (1975) disputed *Lippia* as a larval foodplant.² Undoubtedly a mistake, traceable to Merian (1705), who figured *A. jatrophae* on this species of plant; see text.A = *A. amathea*, C = *A. chrysopelea*, F = *A. fatima*, J = *A. jatrophae*.

(cf. Emmel and Leck, 1970). Local extinctions are frequent. *A. jatrophae* usually persists for awhile after its local congener has disappeared. During these dry times, populations are restricted to moist refugia, and search for these otherwise common species may be frustrating (e.g., Hall, 1925). Although some individuals enter a nonreproductive physiological state during the dry season (O. R. Taylor, Jr., in ms.), there is no evidence for prolonged physiological diapause in *Anartia*. Among other things, their short adult longevity would seem to preclude survival through a long dry season. Groups of adults may seek shelter in the same location (Young, 1979), but they do not form structured aggregations characteristic of many other tropical butterflies.

Adults are also influenced by the availability of nectar sources, and may leave an otherwise suitable area if no flowers are in bloom. They take nectar from many species, especially *Lantana camara* (but *not* from *L. trifolia*; Shemske, 1976; Barrows, 1976; they feed only at the yellow flowers of *L. camara*), *Hyptis mutabilis* and *Sida* sp. (Fosdick, 1973). The seasonal fluctuation in quality, of larval and adult habitats, affects the biogeography (*q.v.*) of *Anartia*.

Based on study of collecting localities and dates, we believe that much of the phenotypic variation seen in *A. fatima* and *A. jatrophae* is due in part to environmental conditions experienced during development.

The population biology of *A. fatima* has been studied in Costa Rica by Young (1972) and Young and Stein (1976), and in Panamá by Silberglid, Aiello and Windsor (in prep.). *A. amathea* has been studied in Ecuador by Fosdick (1973; but cf. Sheppard and Bishop, 1973!). Population sizes differed considerably between the species and studies; in Panamá, dramatic differences in population size were noted from one year to the next. During one year, striking cycles of recruitment from the immature stages occurred on a monthly basis (R. E. S., A. A. and D. M. Windsor, in prep.).

In spite of a sex ratio of 1:1 at eclosion in *A. amathea* ($\delta:\eta = 1.04$, $N=1,957$) and *A. fatima*, ($\delta:\eta = 0.96$, $N=2,281$), samples from *Anartia* populations may be strongly skewed toward one sex or the other. The population of *A. fatima* on Barro Colorado Island, for example, always had a significant preponderance of males, due in part to greater emigration by females in search of oviposition sites (R. E. S., A. A. and D. M. Windsor, in prep.; Organization for Tropical Studies report, cited in Young and Stein, 1976). On the

other hand, Fosdick's population of *A. amathea* in Ecuador was skewed toward females; it is likely that his site contained an abundant supply of larval foodplant on which females oviposited.

Survivorship was low in all populations studied, and it appears that under natural conditions, adult life is short—averaging from one to two weeks (maximum 9 weeks) in the field (R. E. S. and A. A., unpubl.). Young (1972) reported a longevity of 45 days in the laboratory. Adults are subject to heavy predation during their adult lives (see below). There are no field studies of the immature stages of any species.

Palatability and natural enemies

Due to their wide geographic ranges and local abundance, the three mainland species of *Anartia* have frequently been used in experiments on butterfly palatability, mimicry and predator learning. All three species were completely acceptable to the numerous insectivorous vertebrate and invertebrate predators to which they were offered (Table 2). Human subjects report that *A. fatima* have "no taste" or a "walnut flavor" (Emmel, et al., 1968). The predators of adult *Anartia* are those generalist insectivores common in disturbed habitats, especially spiders and insectivorous birds. Larvae probably suffer greatly from predation by social and solitary wasps. We have reared one (unidentified) tachinid parasitoid from a wild *Anartia* larva, but have never encountered viral or bacterial disease during the rearing of over 5,000 individuals.

In spite of their palatability, *Anartia* are often the most common species in the habitats where they occur. The tremendous losses of adults, and probably greater losses of larvae, are more than compensated for by the great fecundity in this genus (see below).

Function of coloration

Various functions have been suggested for the color patterns of *Anartia* species. *Anartia* orient to the sun and bask (Longstaff, 1912; Fosdick, 1973). There is no distal circulation in their wings, so only the colors of the body and wing bases play a role in thermoregulation (see Wasserthal, 1975; Douglas, 1979).

Brower, et al. (1971) present convincing experimental evidence to support the idea that *A. amathea* is an "incipient" Batesian mimic of *Heliconius erato*. Caged predators that tasted, and learned to avoid, *H. erato*, also refused the similar-colored *A. amathea*, even though

Table 2. Palatability tests using *Anartia* species: all three species tested were found to be palatable to all predators.

PREDATOR	PREY	CONDITIONS	LOCALITY	REFERENCE
ARANEAE (Araneidae)				
<i>Argiope argentata</i>	A	field obs.	Panamá (Darién)	R.E.S. & A.A.
<i>Argiope argentata</i>	F	field obs.	Panamá	R.E.S. & A.A.
ORTHOPTERA				
(Mantodea)	F	field obs.	Panamá	R.E.S. & A.A.
(Mantodea)	F	feeding exp.	Costa Rica	Emmel (1972)
HEMIPTERA (Reduviidae)				
<i>Apiomerus</i> sp.	F	field obs.	Panamá	R.E.S. & A.A.
HYMENOPTERA (Vespidae)				
<i>Polistes canadensis</i>	F, larva	field obs.	Panamá	R.E.S. & A.A.
REPTILIA				
<i>Ameiva ameiva</i> (Teiidae)	F	field exp.	Panamá	Boyden (1976)
"several lizard species"	F	field exp.	Costa Rica	Emmel (1972)
AVES				
(Corvidae)				
<i>Cyanocitta cristata</i>	A	lab exp.	Trinidad	Brower & Brower (1964)
<i>Cyanocitta cristata</i>	A	lab exp.	Trinidad	Coppinger (1970)
<i>Cyanocitta cristata</i>	J	lab exp.	Trinidad	Coppinger (1970)

Table 2. continued

(Icteridae)				
<i>Agelaius phoeniceus</i>	A	lab exp.	Trinidad	Coppinger (1970)
<i>Agelaius phoeniceus</i>	J	lab exp.	Trinidad	Coppinger (1970)
<i>Quiscalus quiscula</i>	A	lab exp.	Trinidad	Coppinger (1970)
<i>Quiscalus quiscula</i>	J	lab exp.	Trinidad	Coppinger (1970)
(Thraupidae)				
<i>Ramphocelus carbo</i>	A	lab exp.	Trinidad	Coppinger (1969)
<i>Ramphocelus carbo</i>	A	lab exp.	Trinidad	Brower, et al. (1971)
<i>Ramphocelus carbo</i>	J	lab exp.	Trinidad	Coppinger (1969)
<i>Ramphocelus carbo</i>	J	lab exp.	Trinidad	Brower, et al. (1971)
(Tyrannidae)				
<i>Muscivora tyrannus</i>	A	lab exp.	Trinidad	Alcock (1969)
<i>Muscivora tyrannus</i>	A	lab exp.	Trinidad	Coppinger (1969)
<i>Muscivora tyrannus</i>	A	lab exp.	Trinidad	Brower, et al. (1971)
<i>Muscivora tyrannus</i>	J	lab exp.	Trinidad	Coppinger (1969)
<i>Muscivora tyrannus</i>	J	lab exp.	Trinidad	Brower, et al. (1971)
MAMMALIA (Hominidae)				
<i>Homo sapiens</i>	F	taste test	Costa Rica	Emmel, et al. (1968)

A = *A. amathea*, F = *A. fatima*, J = *A. jatrophae*.

the patterns in which the colors are arranged are very different in the two species. Less convincing is Emmel's (1972) suggestion that *A. fatima* mimics other, striped, *Heliconius* species. *A. fatima* resembles far more closely various *Adelpha*, *Doxocopa*, and other presumably palatable nymphalines.

The wing-bands of *A. fatima* are visible from both above and below, like those of a great many other banded butterflies (e.g., *Graphium kirbyi*, *Cyrestis acilia*, *Limenitis arthemis*, etc.). Such "disruptive" patterns presumably protect their bearers from predators (Platt and Brower, 1968), but the only evidence available to date does not support this hypothesis (Silberglied, et al., 1980). The wings of *Anartia* are brittle and easily fractured; mutilated individuals bearing evidence of unsuccessful attacks by predators, are common (e.g., Longstaff, 1912; see Silberglied et al., 1980).

The wing color patterns of *Anartia* spp. also play important intra- and interspecific communicatory roles between butterflies. These are discussed below under "courtship and mating."

Flight and daily activity

A. amathea and *A. fatima* have a jaunty, somewhat erratic flight that enables them to move about beneath the foliage of low herbaceous vegetation when seeking eclosing females (males) or oviposition sites (females). However, much of their time is spent in more open spaces as they feed at flowers, bask, chase other butterflies, etc. *A. jatrophae* has a strikingly different flight, in which long glides are interrupted by abrupt, mid-air pauses ("... spasmodic... alternate 'start' and 'glide,'" Walker in Brown and Heineman, 1972). Since less time is spent beating the wings, this type of flight requires less energy per unit distance travelled, than that of *A. amathea* and *A. fatima*; it may enable individuals to fly considerably greater distances. When alarmed, *A. jatrophae* seems to use an ascending escape maneuver more often than *A. amathea* or *A. fatima*.

Anartia species are active under sunny conditions, and during light rain. They avoid the dark interior of the forest, and rarely fly in strong winds (Young, 1979). Emmel (1972) plotted morning courtship activity curves for yellow- (young) and white-banded (older) male *A. fatima*, and Young (1972) reported daily oviposition activity of *A. fatima* to be between 10:00 and 13:00 hours.

Courtship and mating

Male *A. fatima* use both 'waiting' and 'seeking' behaviors (Magnus, 1963) to locate females. 'Waiting' males are found sitting on vegetation, often with wings slightly spread, from which they fly to inspect nearly any butterfly that passes. These chases may be quite prolonged, even when chasing other species or conspecific males. While such behavior has often been called 'aggressive' (e.g., Walker, in Brown and Heineman, 1972), we know of no way to differentiate it from simple inspection flights in which the responses of the pursued individual provides information to the pursuer (see Silberglied, 1977). Under crowded conditions in flight cages, groups of males sometimes form 'strings,' each male courting the one ahead. Males often return to the same waiting site after an unsuccessful chase. *A. jatrophae* males seem to prefer lower waiting sites than males of *A. amathea* and *A. fatima*.

When chasing, the male of *A. fatima* attempts to get above and slightly behind the female. If she does not avoid him, the male executes a 'bobbing' flight, during which he may be sending chemical and/or visual signals. Such 'bobbing' pairs persist for up to several minutes, the female descending lower and lower until she alights upon vegetation. The male alights next to the female, and attempts to couple with her by bending his abdomen laterally as he walks forward (Emmel, 1972), but she may still refuse his advances by flying off, or by spreading her wings. A side-to-side motion of the sitting female has been reported as denial behavior in *A. amathea* (Fosdick, 1973).

'Seeking' males fly low into vegetation, where they are often successful in locating and mating with teneral females (Emmel, 1972). Females usually mate during their first two days of adult life, but males generally do not mate until the third day after eclosion (R. E. S. and A. A., in prep.). Males do not mate more than once per day, but may mate on several days in succession. We have known individual males to mate up to nine times and still be capable of producing a spermatophore.

Color and pattern appear to be important stimuli to males seeking females. Preference tests with dummies of *A. fatima* show that males prefer normally-colored females, and that obliteration of either the light bands or red markings reduces the number of approaches (Emmel, 1972; Taylor, 1973). Female *A. fatima* with

yellow wing-bands are less attractive to males than those with white bands. The white band color reflects ultraviolet light more strongly (25% reflection) than does the yellow (14%)⁴; whether this component is important behaviorally remains to be determined. Males of *A. amathea* mate far less frequently with living females whose red color has been obliterated (R. E. S. and A. A., in prep.), than with red control females. Since *A. amathea* and *A. fatima*, like some other butterflies but unlike most other insects, see red (Bernard, 1979), it is not surprising that this color may be an important social signal. It has also been suggested that the black spots of *A. jatrophae* may be important as a visual signal (Atsatt, 1968).

Female mating behavior has been studied in *A. amathea* and *A. fatima* (R. E. S. and A. A., in prep.). Virgin females, isolated in flight cages from males, frequently approached other females in what may be "solicitation" behavior, but of course this rarely would happen in nature.

The outcome of most courtships of non-teneral females is probably determined primarily by female acceptance/rejection behavior (Taylor, 1972; R. E. S. and A. A., in prep.). Females of *A. amathea* mate assortatively, preferring conspecific males, but females of *A. fatima* do not discriminate between their own males and those of *A. amathea*. In *A. amathea*, females do not discriminate between conspecific males that had the red color obliterated, and normally-colored control males. The asymmetry of assortative mating, that results from these differences in female behavior of *A. amathea* and *A. fatima*, has evolutionary and ecological consequences at the juncture of the two species' ranges in eastern Panamá.

Copulation generally lasts from thirty minutes to one hour, but may be prolonged to as much as twelve hours. Young and Stein (1976) suggest that female *A. fatima* mate but once, Ehrlich and Ehrlich (1978) report a mean of 0.92 spermatophores per female in *A. amathea* (N=12, with no more than one per female) and Andersen (1969) reported a small number of female *A. fatima* with two spermatophores. Ehrlich and Ehrlich (1978) also suggest that *Anartia* might be a species capable of absorbing spermatophores:

⁴ Reflectance was measured densitometrically (Silberglied, 1976); on extreme yellow and white individuals. Emmel's (1972) description is misleading because, among other things, the television camera he used adjusts contrast automatically. Reflectance comparisons made with such a camera setup (Eisner, et al., 1969) are qualitative at best.

THE LIFE CYCLE

Oviposition and Larval Foodplants

Females in search of oviposition sites fly within a few centimeters of low vegetation, and land frequently and briefly upon a variety of plants. Eggs are laid singly, usually, but not always, on the larval foodplant (Table 1). *A. chrysopelea* has been seen ovipositing on *Tradescantia* sp. (Dethier, 1941), *A. jatrophae* on *Cyperus diffusa*, *Oldenlandia corymbosa* and *Polygala verticillata*, and *A. fatima* on "dead twigs, moss, rocks, walls, dry leaves, logs" (Young and Stein, 1976), "grasses, especially *Oplismenus* spp." (Young, 1972), *Croton hirtus*, *Chaptalia nutans*, garden hoses and cement walkways — none of which are acceptable larval foods. In the laboratory, *A. fatima* deposited more eggs on cage walls than on the *Blechnum brownei* leaves provided. Apparently the only requirement for an oviposition site is that it be *near* the correct foodplant, but the stimuli important in eliciting oviposition behavior remain unknown (cf. Young and Stein, 1976). We have never seen any species of *Anartia* oviposit in an area that did not contain a real larval foodplant.

Anartia species have unusually high fecundity. A single female may lay several hundred eggs over the course of a few days (Young, 1972; Silberglied and Aiello, in prep.). Ehrlich and Ehrlich (1978) report that female *A. amathea* have approximately 100 eggs per ovariole, or a potential 800 eggs per female. Considering the sort of mortality for which such fecundity must compensate, the larva that survives to adulthood must be rare indeed.

The larval foodplants of *Anartia* are listed in Table 1. While *A. fatima* and *A. amathea* accept *Blechnum brownei* and *B. costaricense* as foodplants in Panamá, in their natural habitat they would be less likely to encounter *B. costaricense*, a forest species. Neither *A. amathea* nor *A. fatima* will feed on *Nelsonia brunellodes*, another member of the same family, that often grows with *B. brownei* in Panamá.

A. jatrophae has been reared upon numerous and diverse foodplants (see Table 1). Assuming that this pattern is real and not an artifact of limited data, we find it interesting that *A. jatrophae*, the most widespread of the three species, also has the broadest range of foodplants. This flexibility may enable it to coexist side by side with its congeners, with less direct competition for food. Furthermore, *A.*

jatrophae's range extends to higher latitudes in both hemispheres than any other congener; its more polyphagous nature may be compared with the similar patterns found for temperate papilionids by Scriber (1973).

Immature stages

The first reliable account of the immature stages of *Anartia* was that of Müller (1886), who described five larval instars and the pupa of *A. amathea*, and correctly identified the foodplant family as Acanthaceae. Earlier authors (Merian, 1705, copied by Sepp, 1852-1855 — see Müller, 1886; Seitz, 1914) erroneously reported the foodplant for *A. jatrophae* as "Manihot," and figured adult butterflies together with a pubescent moth-like larva lacking scoli, and a pupal exuvium of dubious affinity. Later accounts of the immature stages are given for *A. jatrophae* by Scudder (1893), Dethier (1941), Klots (1951), Riley (1975) and Rawson (1976); for *A. amathea* by Riley (1975); for *A. chrysopelea* by Dethier (1941); and for *A. fatima* by Young and Stein (1976). Nothing is known concerning the immature stages of *A. lytrea*.

Eggs

The eggs (Figure 6) of *A. amathea* and *A. fatima* are yellowish green, 0.65 to 0.70 mm in diameter, slightly taller than wide, and have eleven to thirteen longitudinal wax-crested ribs which extend to within 15 degrees of the upper pole, which is centered on the micropyle. The ventral surface is flat. The ribs are perpendicular to and rest upon 40-50 low ridges with which the egg is banded. The number of vertical ribs is variable within species and even among the eggs of a single female (Dethier, 1941). The eggs of *A. jatrophae* are similar (Dethier, 1941; Rawson, 1976), but those of *chrysopelea* are wider than they are high (Dethier, 1941). We were unable to distinguish the eggs of *A. amathea* and *A. fatima* from one another.

Larvae

While *Anartia* larvae have been described by several authors, only Dethier (1941) used morphological terminology⁵ precise enough for

⁵In their accounts of larval armature, some authors refer to setae as "hairs" or "spines," and to scoli beset with numerous setae as "branched spines." Many other inaccuracies are found in several published larval descriptions. Our terminology follows that of Peterson (1962); bilaterally arranged thoracic and abdominal armature units (e.g., scoli, verrucae, chalazae, setae) are described in the singular.

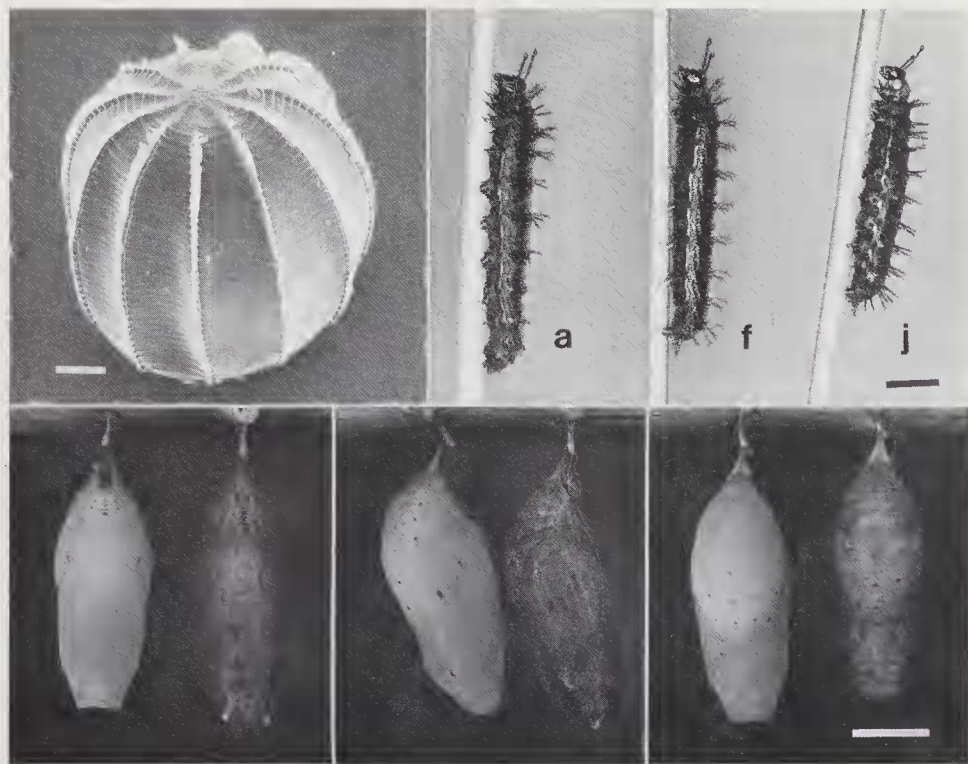


Figure 6. Developmental stages of *Anartia* spp. Upper left: egg of *A. fatima*; scale = 0.1 mm; scanning electron micrograph by E. Seling. Upper right, lateral view of three larvae: a = *A. amatheia* (several abdominal scoli missing), f = *A. fatima* (both last instars), j = *A. jatrophae* (penultimate instar), scale = 5 mm. Below: *A. fatima*, pupae, showing color variation, ventral lateral and dorsal views; scale = 5 mm.

comparative work. Since the known larvae differ little between species, the following account may be considered generic except as noted.

FIRST INSTAR (based primarily on *A. fatima*: *Head* (Figure 7): well-sclerotized, scoli lacking; *labrum* emarginate, bearing six pairs of setae; *frons* triangular, bearing three pairs of setae, ventral margin concave; two pairs of *adfrontal setae*, upper pair shorter than lower; *epicranium* rounded, each side bearing five long setae; three setae associated with the *stemma* ("ocelli") and one with the *antennae*, as figured. *Thorax*: ventral *eversible prothoracic gland* between the legs and head; *cervical shield* with four pairs of setae, three dark pairs directed forwards, and one pale, thinner pair, directed backwards; *subdorsal chalaza* on meso- and metathorax; *supraspiracular chalaza* on pro-, meso- and metathorax, that of prothorax bearing two setae; *subspiracular chalaza* on meso- and metathorax, situated slightly above plane of spiracles; *prespiracular chalaza* on prothorax, bearing two setae; a chalaza located between subspiracular and subventral chalazae on meso- and metathorax may be serially homologous with the prothoracic prespiracular chalaza; *subventral chalaza* on pro-, meso- and metathorax, that of prothorax bearing two setae. *Abdomen*: first segment darker than the others; *subdorsal chalaza* on segments 1-9, a small chalaza between, and posterior to, the subdorsal and subspiracular chalaza on segments 1-8 (situated posterior to subdorsal chalaza on segment 8); *supraspiracular chalaza* on segments 1-9; *subspiracular chalaza* on segments 1-9, that of segment 9 bearing two setae; *subventral chalaza* on segments 1-10 (segment 10 with two, located posteriorly); *suranal plate* rounded; *prolegs* on segments 3-6 and 10, well developed; *crochets* uniserial, uniordinal, arranged in a circle; *setae* (one per chalaza except as noted) microscopically serrate, and curved anteriorly.

SECOND INSTAR (based on *A. amathea*, *A. fatima* and *A. jatrophae*): *Head* (Figure 7): as in first instar except for addition of a pair of epicranial scoli, and secondary setae in epicranial, frontal, anterior, and ocellar areas. *Thorax*: ventral *eversible prothoracic gland* between legs and head; *cervical shield* with four pairs of setae, two dark pairs and two pale pairs; *subdorsal scoli* on meso- and metathorax; *supraspiracular verruca* on pro-, meso- and metathorax; *subspiracular scoli* on pro-, meso- and metathorax; *prespiracular verruca* on prothorax; a verruca located between subspiracular and

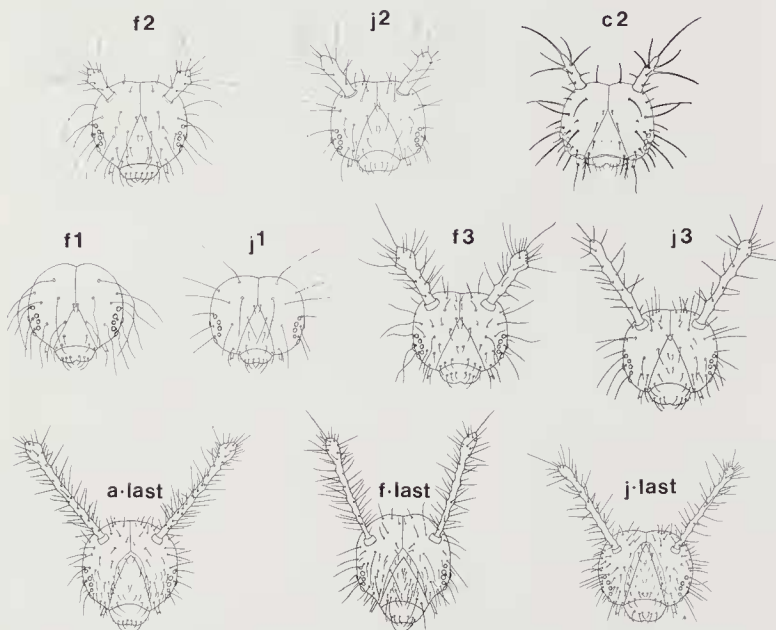


Figure 7. Head capsules of *Anartia* spp. a = *A. amathea*, c = *A. chrysopelea*, f = *A. fatima*, j = *A. jatrophae*. Numbers on figure indicate instar number; numbers in brackets are head capsule widths in mm. f2 [width of head capsule = 0.6 mm], j2 [0.5], c2 [0.575, measurement and figure from Dethier, 1941], f1 [0.4], j1 [0.4], f3 [1.0], j3 [0.9], a-final [2.5], f-final [3.0], j-final [2.7].

subventral scoli on meso- and metathorax may be serially homologous with the prothoracic prespiracular verruca; *subventral scoli* on pro-, meso- and metathorax. *Abdomen*: *mediodorsal scoli* on segments 1–8 (segment 8 with two, one anterior, one posterior); *subdorsal scoli* on segments 1–8; *supraspiracular scoli* on segments 1–10; *subspiracular scoli* on segments 1–8; *subventral scoli* (small) on segments 1, 2 and 7; pair of *subventral verrucae*, one anterior, one posterior, on segments 3–6; pair of posterior subventral verrucae, one above the other, on segment 10; *suranal plate* triangular; *prolegs* as in first instar; *crochets* uniserial, triordinal, arranged in a mesoseries; *setae* numerous on each scoli.

MORPHOLOGICAL DIFFERENCES BETWEEN FIRST AND SECOND INSTARS: In the second instar⁶, scoli and additional setae appear on the head (Figure 7); the chalazae of the first instar are replaced by scoli and verrucae; the setae are no longer serrate; the central pair of setae on the cervical shield is pale; a prothoracic subspiracular scolus appears (no prothoracic subspiracular chalaza in the first instar); mediodorsal armature appears on abdominal segments 1-8; the following armature is lost: subdorsal chalaza on segment 9, the small chalaza between and posterior to the subdorsal and supraspiracular chalazae on segments 1-8, the subspiracular chalaza on segment 9, and the subventral chalaza on segments 8 and 9; a supraspiracular scolus appears on segment 10; the subventral chalaza on segments 3-6 is now a pair of scoli; the suranal plate becomes triangular; the crochets become triordinal and are arranged in a mesoseries.

THIRD AND SUBSEQUENT INSTARS: The head scoli are clubbed (slightly more so in *A. amathea* and *A. fatima* than in *A. jatrophae*) in the third through final instars (Figure 7). The head width increases by factors of 1.5 (*A. fatima*), and 1.6 (*A. amathea* and *A. jatrophae*) (see Figure 8). The adfrontal sutures become conspicuous in the final instar, by which time the body is black, the scoli are reddish brown, and there are often coarse longitudinal stripes composed of light dots. The prothoracic eversible gland is present in all instars.

The interspecific differences in larval morphology are very subtle. A detailed, comparative larval study must await the discovery of the larva of *A. lytrea*, and the collection of new material of *A. chrysopelea*.

The number of instars is variable: *A. amathea* from Colombia had five instars (Müller, 1886; R. E. S. and A. A.); *A. fatima* from Panamá had six (A. A. and R. E. S.); from Costa Rica five (Young and Stein, 1976); *A. jatrophae*⁷ from Panamá had five (A. A. and R.

⁶Dethier's (1941) description, of a second instar *A. jatrophae* from Cuba, differs from ours in the number of scoli on abdominal segments 8-10, and in the reported absence of a subspiracular scolus on the prothorax. From his account of the first four instars of *A. chrysopelea*, the larvae of that species are very similar in setal arrangement to the three described above. However, he reports that the setae of the first instar larva "... do not arise from conspicuous sclerotized areas ..."

⁷Rawson (1976) reported three instars for *A. jatrophae* from Florida, but from his illustrations it is probable that he missed one or more instars; his "third" instar is probably a fifth or sixth. The sum of Rawson's development times is also unusually short. Further rearing in Florida should be done to corroborate his account.

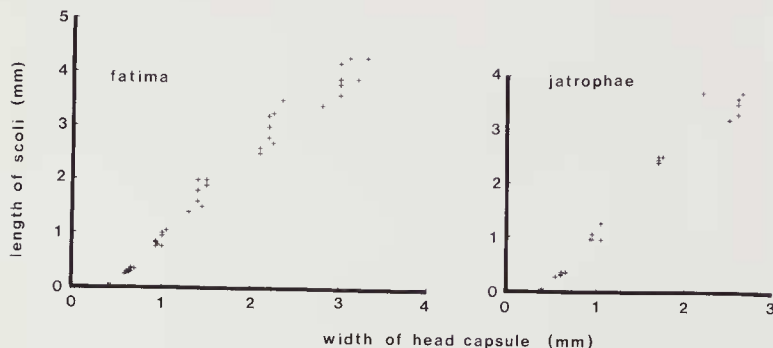


Figure 8. Dimensions of head capsules and scoli of the larvae of *A. fatima* and *A. jatrophae*, reared individually. Note that *A. jatrophae* has one less instar, but grows more per instar, than *A. fatima*. However, the final larval head capsule size of *A. jatrophae* is not quite as large as that of *A. fatima*. [Instar 1 lacks scoli.]

E. S.). Development times for *A. amathea*, *A. fatima* and *A. jatrophae*⁷ in Panamá are given in Table 3 (reared individually) and Figure 9 (reared under crowded conditions). Similar times are given for partial life cycles of *A. jatrophae* by Dethier (1941) and Rawson (1976), and for *A. chrysopelea* by Dethier (1941). Young (1972) reported 28 days, and Young and Stein (1976) reported 46–49 days, both for *A. fatima* in Costa Rica. Under identical rearing conditions, *A. jatrophae* takes less time and fewer instars to develop to adult than does *A. fatima* (Table 3).

Table 3. Development time (days) for two species of *Anartia*, reared as isolated individuals under identical conditions in Panamá. The difference between total mean development times for the two species is significant ($t = 5.599$, $df = 21$, $p < .0005$).

STAGE	<i>A. jatrophae</i> (N=7)		<i>A. fatima</i> (N=16)	
	mean	s.d.	mean	s.d.
egg	3.86	0.38	5.06	0.25
instar 1	4.00	0.00	3.25	0.45
instar 2	3.14	0.38	3.06	0.25
instar 3	2.43	0.53	2.81	0.40
instar 4	3.29	0.49	3.13	0.50
instar 5	7.14	0.38	3.31	0.60
instar 6	—	—	6.88	0.84
pupa	7.86	0.38	6.88	0.50
TOTAL	31.72	0.76	34.38	1.54

Pupae

A larva nearing pupation wanders for about one day, then prepares a silk pupation platform several centimeters above the ground on the underside of a leaf or twig. Platform making usually begins in the late afternoon or early evening, and is quickly followed by spinning of the silk stalk from which the pupa will be suspended. During platform making and stalk spinning, larvae evert the whitish gland located ventrally on the prothorax between the legs and head. The function of this gland is not known. Once the silk stalk is completed, the larva walks forward until its tenth segment prolegs are positioned over it. These prolegs are then used to pull and shape the stalk before they finally clamp onto it, and support the larva during its final molt. By midnight most larvae have let go with all but the tenth segment prolegs, and now hang in a "J" position until 8 or 9 AM, when ecdysis takes place.

In the laboratory, larvae hang from the cage cover to pupate. Under crowded conditions, freshly-formed pupae may be cannibalized by hungry final instar larvae.

Pupae of *A. amathea* (Müller, 1886), *A. fatima* (Young and Stein, 1976), and *A. jatrophae* (Scudder, 1893; Wolcott, 1951; Rawson, 1976) are 15–22 mm long, smooth, spindle-shaped and without protuberances. They are usually translucent jade green in color, with dark spots (Figure 6; see also Young and Stein, 1976) in the same positions occupied by scoli in the final larval instar, plus a few additional dark marks on the wings. Occasional individuals of all three species are black (Scudder, 1893; A. A. and R. E. S.).

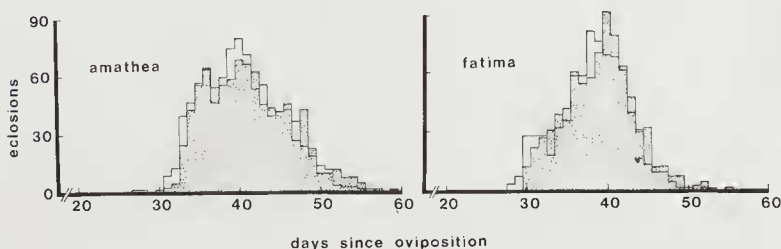


Figure 9. Development times of male and female (stippled) *A. amathea* (N=1,764) and *A. fatima* (N=1,579), reared under crowded conditions (up to 20 larvae per container).

The pupal period usually lasts six to eight days in the three species we have studied (see also Rawson, 1976; Young, 1972; Young and Stein, 1976). A day or two before eclosion, color changes can be seen through the pupal skin. The eyes turn yellow and finally brown, and the wings become pale brown (in *A. jatrophae*) or black (*A. amathea* and *A. fatima*). In *A. fatima* the wing-bands show clearly by the morning of eclosion. Adults emerge during the morning and are ready to fly within one to two hours.

BIOGEOGRAPHY

The three distinctive evolutionary lines of the genus *Anartia* have well-defined and interesting geographic distributions (Figure 10). *A. lytrea* and *A. chrysopelea* are West Indian endemics on Hispaniola and Cuba, respectively. (*A. chrysopelea* is also known from the Isle of Pines, Swan Island, and southern Florida.) *A. fatima* and *A. amathea* are widely distributed in tropical Central and South America, respectively. *A. jatrophae* is ubiquitous throughout all the warm regions of the Western Hemisphere, including the southern United States, the Bahamas and West Indies, all of Central and most of South America, to about 30 degrees north and south latitude. It has been difficult to determine the limits in some areas because of the tendency of collectors not to collect common species once a series has been obtained. Since all species can be collected around human habitations, many collectors do not bother with them soon after arrival in the tropics. Another problem has been the profusion of mislabelled specimens and erroneous reports, such as *A. fatima* from "Brasil," and *A. amathea* from "Mexico" (da Silva, 1907) and "Havane" (Lucas, 1857). The southernmost limits of *A. jatrophae* and *A. amathea* are poorly documented; neither species occurs in Chile.

Within these broad distributions, *Anartia* spp. are restricted to moist, or at least not very dry, disturbed habitats where their larval foodplants grow. Distributions may change markedly during the year in areas having pronounced dry seasons. Local extinctions of many populations occur through the dry season, with recolonization following the start of the rains. For example, during 1977, *A. fatima* went extinct throughout most of central and southern Panamá, with occasional individuals remaining at isolated refugia (including dripping air conditioners and lawn sprinklers), but with a



Figure 10. Geographical distributions of *Anartia* species. See "Biogeography."

substantial population remaining active on the moister Caribbean side of the isthmus. Within two months after the rains began, the species had reestablished itself in most of its former habitats.

All species of *Anartia* are highly vagile. Based on our study of the Barro Colorado Island population, it appears that females of *A. fatima* emigrate more than males do. The ecological adaptations of *A. fatima* as a colonizing species have been summarized by Young (1972) and Young and Stein (1976). *A. jatrophae*, with its gliding flight similar to that of many migratory species, appears to be the most vagile, for it usually recolonizes former habitats long before *A. fatima* arrives. It also has a wider geographic range, and its populations, while variable, are not strongly differentiated from one another, suggesting considerable gene flow. Vagrants of all species fly considerable distances, and occasionally establish local, temporary populations beyond the normal range. For example, *A. fatima* reaches Kansas (Howe, 1975), *A. jatrophae* reaches Kansas and southern New England (Ehrlich and Ehrlich, 1961), *A. chrysopelea* has turned up in southern Florida on at least two occasions (Anderson, 1974; Bennett and Knudson, 1976) and possibly once on Antigua (Fruhstorfer, 1907), Godman and Salvin's (1882) record of *A. lytrea* on Jamaica, while unconfirmed (Brown and Heineman, 1972), is certainly within the realm of possibility, and *A. amathea* "... occurs sporadically ... on Antigua, Grenada and Barbados ... no doubt a vagrant ... sometimes established for short periods (Godman and Salvin, 1896; Riley, 1975).

The distributions of all *Anartia* species, except *A. jatrophae*, are strictly allopatric of one another. *A. jatrophae* coexists with all; it is a better colonizer, utilizes a wider array of larval foodplants (Table 1), takes less time to develop (Table 3), and withstands drier conditions. Such correlation of ecological distinctness with coexistence illustrates well the concept of limiting similarity of sympatric congeners, and their comparative ecology would be worth a more detailed study (see also Young and Stein, 1976).

EVOLUTION

Relationships to other genera

Young and Stein (1976) reported the "outstanding discovery" that the immature stages of *A. fatima* are similar to those of *Siproeta*, and suggested a close relationship between the two genera. This similarity, which involves the larval foodplants, egg and larval mor-

phology, and open discal cell in both fore- and hindwing, had been discovered and published ninety years earlier by Müller (1886; see also Brown and Heineman, 1972). While we agree with such an assessment, we want to take this opportunity to point out that this section of the subfamily is replete with genera of uncertain affinity, and we feel it is unwise to speculate further on phylogenetic positions until a broad, modern generic revision of the Nymphalinae, employing larval and biological as well as adult characters, is undertaken.

Evolution within the genus

Anartia clearly contains three distinct phylogenetic lines:

- (1) *A. amathea* and *A. fatima* probably represent a pair of sister-species, derived from a widespread neotropical ancestor. We envision a scenario in which the populations of this ancestor were isolated from one another during the Tertiary subsidences of the Panamanian isthmus, after which time the distinctive colors and patterns of the two species evolved. The secondary contact and occasional hybridization between *A. amathea* and *A. fatima* in the Darien represents a recent event in geologic time, the consequences of which are of considerable interest.
- (2) *A. chrysopelea* and *A. lytrea* probably represent another pair of sister-species, derived from a common ancestor (Bates, 1935). Their physical isolation on separate islands probably fostered their differentiation.
- (3) *A. jatrophae* is a widely-distributed species of great geographic variation. Tendencies toward the formation of distinct, geographically isolated populations are thwarted by the high vagility of individuals.

These three species-groups differ from one another in only a few morphological characters. It is not possible at present to decide which character states are plesiomorphic, and which derived, for these features. For this reason we do not feel it would serve a useful purpose to present speculations on the branching sequence within the genus.

DEPOSITION OF SPECIMENS

Voucher specimens of the immature stages of *A. amathea*, *A. fatima* and *A. jatrophae* have been deposited in the Museum of Comparative Zoology (MCZ). All adult specimens illustrated,

except for *A. lytrea* (American Museum of Natural History [AMNH]), are in the MCZ collection. F1 hybrids have also been deposited with G. B. Small, K. S. Brown, the Museo de Historia Natural "Javier Prado," the Peabody Museum (Yale University), the AMNH, and the National Museum of Natural History (Smithsonian Institution), as well as the MCZ.

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